

SUBDIVISION OF THE LOWER PALAEOZOIC ARTICULATE BRACHIOPOD FAMILY TRIPLESIIDAE

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ABSTRACT. Reconsideration of the form of the triplesiid pseudodeltidium, which has been used as a basis for subdivision into subfamilies, together with the distinct forms of the forked cardinal process, indicates that while these criteria do form useful bases for generic distinction, variation both of combinations of characters and of characters within some genera and species mitigate against any meaningful subdivision of this intriguing and genetically plastic brachiopod family. A recent proposal to establish families of Triplesiacea based on shell ornamentation is shown to be similarly flawed, and the view is taken that at present the genera are best assigned to the single undivided family Triplesiidae.

ALTHOUGH the varied external appearance of the triplesiid brachiopods initially led to species being placed in such disparate genera as *Atrypa*, *Orthis*, *Rhynchonella*, *Spirifer* and *Strophomena*, the combination of strong fold and sulcus, straight hinge-line and short interarea in *Atrypa extans* and other species led Hall (1859) to erect the genus *Triplesia*. This was before any internal structures were known; as knowledge of the valve interiors accumulated, the discovery of the characteristic cardinalia with its long, forked cardinal process (Pl. 1, figs 1, 8, 13) served to confirm the closely knit nature of the group. Schuchert (1913) formally recognized the group as a Subfamily (Tripleciinae) of the Strophomenidae. The marked differences between this subfamily and other strophomenids prompted Öpik (1932) to raise the group to familial level. The distinctive combination of morphological characters was further emphasized by the single family being accorded the status of superfamily by Cooper (1944) and order by Moore (1952), although the latter designation was reduced to a suborder by Muir-Wood (1955) and was accepted as such for the brachiopod *Treatise* (Wright 1965).

Ulrich and Cooper (1936, p. 331), applying the thesis that the family characters of brachiopods are found principally in the dorsal interior and in the region around the ventral beak, noted that the features of the cardinalia were the more persistent, 'presenting practically identical structures in each of the genera'. At the same time they recognized that the genera were distinguished by the characters of the exterior, i.e. ornamentation, plication and shell outline. These characters were in fact the only ones used for generic differentiation until Amsden (1968) established the genus *Placotriplesia*, which he distinguished from *Triplesia* by its pseudodeltidium, which is flat, or at least flush with the interarea, and lacks the median fold seen on that of *Triplesia*. This morphological character was then used to subdivide the family for the first time: into the Placotriplesiinae, containing only *Placotriplesia*, and the Triplesiinae, containing the other ten genera. The two species initially included in *Placotriplesia* were *Triplesia praecipita* and *T. juvenis* (both Ulrich and Cooper 1936), from the St Clair Limestone, in which the former is common and the latter known only from a single specimen. Two species tentatively assigned to the genus by Amsden, *T. waldronensis* (Miller and Dyer) and *T. rostellata* Ulrich and Cooper from the Waldron Shale, were subsequently confirmed by him as lacking the pseudodeltidial fold (Amsden 1971, p. 149).

The morphological term *monticulus* (Cooper and Grant 1974) has recently been applied to the median fold which characterizes the pseudodeltidium in most triplesiacean stocks (Wright and

Jaanusson 1993). Examples of the two contrasting styles of pseudodeltidia are illustrated here for *Plectotreta* and *Ogmoplectia*, the former possessing a well-developed monticulus (Pl. 1, fig. 3), which is lacking in the latter (Pl. 1, fig. 2).

The institutional abbreviations for the repositories of the specimens figured in Plate 1 are: BMNH, The Natural History Museum, London; IGT, Institute for Geology, Tallinn; RMS, Riksmuseum, Stockholm; USNM, National Museum of Natural History, Smithsonian Institute, Washington D.C.

MORPHOLOGICAL VARIATION IN TRIPLESIIIDS

The monograph on Silurian brachiopods from Arkansas and Oklahoma, USA, by Amsden (1968) included a revision of the diverse triplesiid stocks of the St Clair Limestone that were described by Ulrich and Cooper (1936). In this monograph three subgenera of *Onychotreta* Ulrich and Cooper were proposed along with *Placotriplesia* and the subfamily Placotriplesiinae. Concern was expressed by Wright (1972) that *Onychotreta* represented a very plastic and commonly deformed stock of highly variable form for which, in view of the distribution of all six *Onychotreta* species at one locality (Wright 1972, table 1), there was doubt over the reality of the species let alone the subgenera. The point was made in that paper that there is a 'variation of variation' (Wright 1972, p. 8) with some stocks having much greater plasticity than others, a point which has been recently illustrated from living populations of *Terebratalia transversa* by Schumann (1991). The variation of the St Clair triplesiid stock at the cited locality produced a further generic problem over a single ventral valve with the elongate form of *Onychotreta* for which Ulrich and Cooper (1936, p. 335) erected a separate species, *Brachymimulus elongatus*, this generic assignment being on the basis of the 'strong, wide (ventral) fold'. Amsden (1968, p. 38) felt that this was possibly a morphological variant of *Onychotreta plicata*, although he accepted the species questionably as *Brachymimulus* (Amsden 1968; Amsden and Barrick 1988); I would regard the specimen as a variant of

EXPLANATION OF PLATE I

- Figs 1, 8, 13. *Triplesia* sp. Haraldstangen, east coast, Hurum, Norway; Ordovician (Ashgill), Langåra Formation; silicified hinge regions showing keeled cardinal process, clearly separated brachiophores and sockets of dorsal valves, and their relationships to the teeth and dental plates of the ventral valves. 1, antero-lateral view of RMS Br136900. 8, 13, anterior views of RMS Br136901 and RMS Br136902. All $\times 8$.
- Fig. 2. *Ogmoplectia* sp. IGT Br4350; Korgessare Quarry, Island of Hiiumaa, Estonia; Ashgill, Vormsi Stage (F 1b); postero-dorsal view of conjoined valves showing ventral interarea with flush pseudodeltidium lacking a median fold (monticulus), $\times 3$.
- Figs 3-4, 7. *Plectotreta lindstroemi* Ulrich and Cooper, 1936. Gotland, Sweden; Silurian; locality and horizon unknown; 3, RMS Br99526, dorsal view of ventral valve, showing well-developed monticulus. $\times 4$. 4, 7, RMS Br99525; ventral and antero-ventral views of dorsal valve showing features of the grooved cardinal process and brachiophores. All $\times 5$.
- Figs 5-6. *Streptis* cf. *monilifera* (M'Coy). USNM 454645; Osmundsberget, Dalarna, Sweden; Ashgill, Boda Limestone; anterior and dorsal views to show sinusoidal anterior commissure. Both $\times 5$.
- Fig. 9. *Ogmoplectia* sp. nov. RMS Br136899; Ireland; Ashgill (Cautleyan), Portrane Limestone; anterior view of silicified dorsal valve to show grooved cardinal process and brachiophores, $\times 4$.
- Figs 10, 12, 15. Triplesiid gen. et sp. nov. RMS Br13445; Kallholn Quarry, Dalarna, Sweden; Ashgill, Boda Limestone; dorsal, ventral and anterior views of conjoined valves. All $\times 2$.
- Figs 11, 14. *Streptis grayii* (Davidson). BMNH B.8072 (Davidson Colln); Gotland, Sweden; 'Wenlock', locality and horizon unknown; details of cardinalia in a disarticulated dorsal valve. 11, postero-ventral view showing cardinal process hood, forked cardinal process and brachiophores. 14, antero-ventral view showing grooved nature of cardinal process. Both $\times 5$.



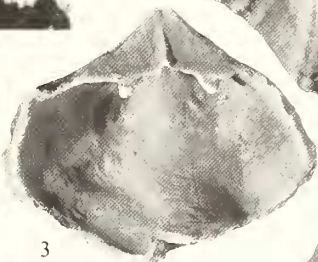
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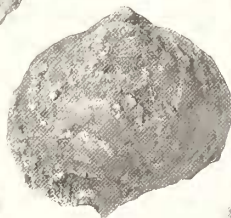
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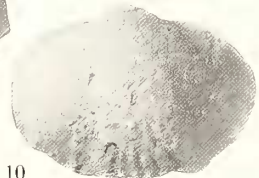
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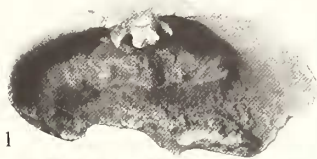
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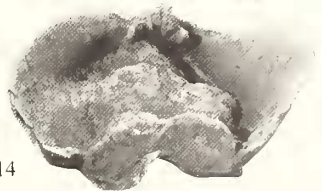
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Onychotreta. In other stocks, such fold reversion is standard and therefore appears to be a valid generic character. *Brachymimulus* is separated generically from *Triplesia* on the criterion of having a ventral and not a dorsal fold; the recently erected *Paraonychoplecia* Percival, 1991, is similarly differentiated from the older *Onychoplecia* by its ventral fold.

Regarding *Placotriplesia*, variation in the development of the median fold on the pseudodeltidium in various triplesiids further raised doubts as to whether a genus and subfamily should be defined on this single character (Wright 1971). Examples cited in that paper of the variation of the pseudodeltidial fold included: the sample from the Ashgill Portrane Limestone of *Oxoplecia* cf. *plicata* (Wiman) in which the median fold was only occasionally developed; a sample of *Oxoplecia* sp. from the Chair of Kildare Limestone (Ashgill, Ireland) again predominantly without the fold; and the species *Oxoplecia filosa* and *O. multicostellata* described by Cooper (1956) from rocks of Caradoc age in Oklahoma and Virginia, USA, respectively in which the fold of the young stages is lost in the adult. Amsden (1974), in his redescription of the Ashgill *Cliftonia tubulistriata* (Savage) from Missouri, USA, recorded that in this form also the pseudodeltidial fold may or may not die out towards the front of the pseudodeltidium. Amsden's assertion (1973, pp. 253, 273) that 'Wright's observation that the type species of *Placotriplesia* (*P. praecipta*) has a pseudodeltidial fold is incorrect' needs to be corrected. The text on this species (Wright 1971, pp. 342–343) is as follows: 'Ulrich and Cooper (1936, p. 333) state that the median fold is possessed by "well preserved specimens", the implication being that any absence of the structure is a reflection of preservation. But Amsden (1968, p. 41) maintains that its absence in the case of *T. praecipta* is not the result of preservation, a view which my own studies of this and other triplesiid species would support. With some reservations, Amsden's observation of the flat nature of the pseudodeltidium in this species then is essentially acceptable.'

THE CARDINALIA-PSEUDODELTIDIAL COMBINATION

In the typical systematic description of the triplesiid species, the cardinal process is implied or described simply as being forked, or perhaps further modified as being long, short or recurved. Ulrich and Cooper (1936, p. 333) additionally comment on variation within a species as ranging from 'rather stout' to 'comparatively slender'. A basic morphological difference in the cardinalia only came to light in 1964 when the strikingly different cardinal processes of species of *Triplesia* and *Oxoplecia* from the Cautleyan Portrane Limestone of Ireland (Wright 1964, pl. 11, figs 9, 12) were respectively described as having the fork fused proximally into a single unit, or deeply cleft with each prong fused more with the adjacent brachiophore than with the other prong. The two types, here represented in Plate 1, figures 8 and 9, were subsequently designated as 'keeled' or 'grooved' (Wright 1971, p. 354) and in attempting to assess the taxonomic value of the structures of the postero-median part of the valves, the point was made that the typical Portrane *Oxoplecia* with a grooved cardinal process also possesses a smooth pseudodeltidium. Although this was not considered by Amsden, his sections of *Placotriplesia praecipta* (1968, text-figs 23B–C, 24D–E) show that its process is also of the grooved type. Moreover, the lack of a cardinal process hood is also common to these two forms.

The basis for a subfamilial division on the combination of smooth pseudodeltidium and grooved cardinal process on the one hand and of fold-bearing pseudodeltidium and keeled cardinal process on the other seemed plausible. However, the presence of an *Oxoplecia* sp. from the Ashgill Kildare Limestone of Ireland, which in some specimens combined a grooved cardinal process with a pseudodeltidial fold effectively precluded a subfamilial division based on the linkage of the *Placotriplesia* characters (Wright 1971, p. 354); but the combination of characters does appear useful at a generic level. In contrast to my initial views (Wright 1971) I am now convinced of the soundness of Amsden's genus and its usefulness in biostratigraphy.

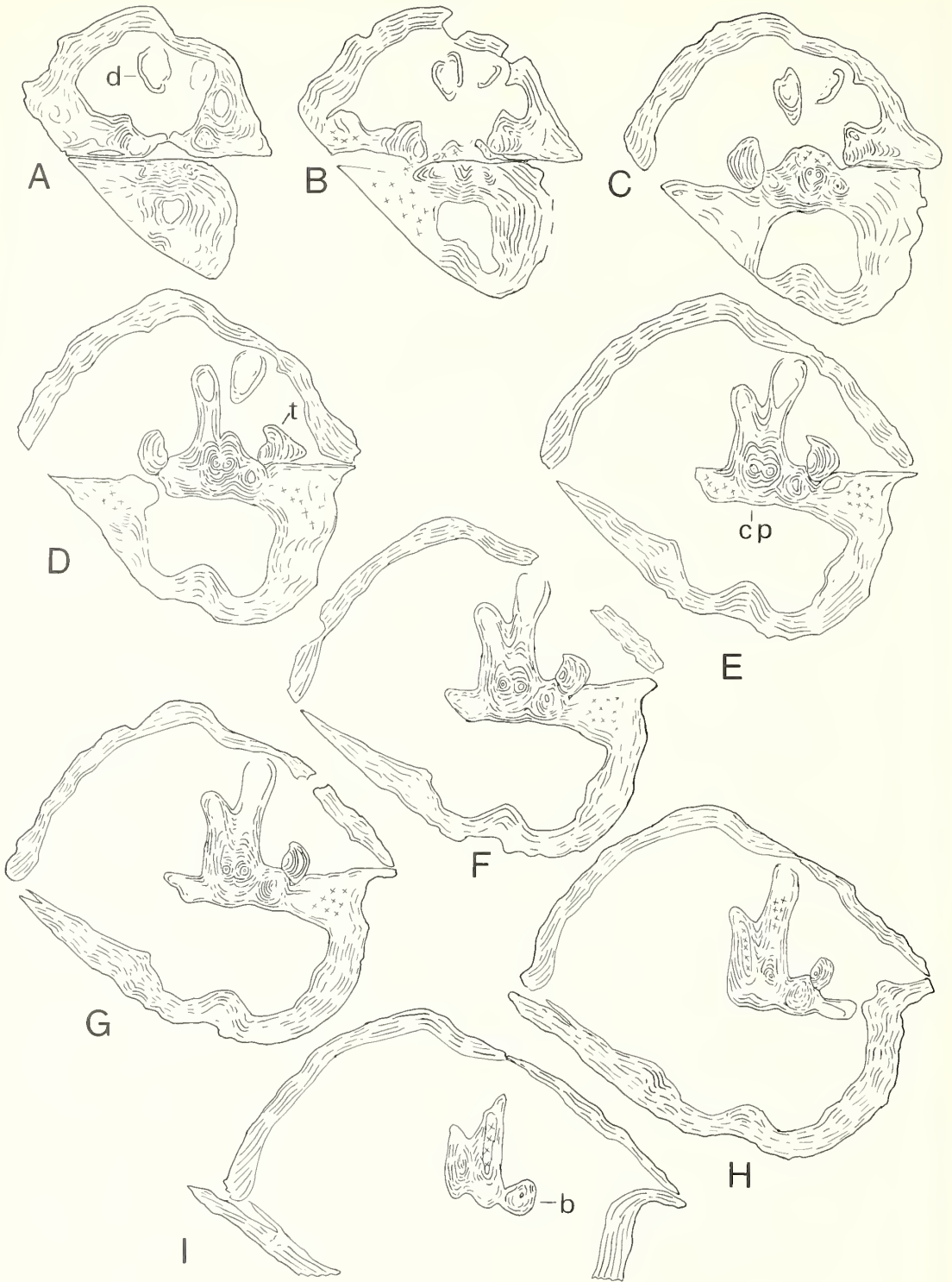
To accommodate species such as the forms noted above from Portrane and Kildare hitherto placed in *Oxoplecia* but which differ from that genus notably in the possession of a grooved cardinal

process and a predominantly smooth pseudodeltidium, a new genus, *Ogmoplecia*, has been established (Wright and Jaanusson 1993). This is a widespread although rarely abundant form in the Ashgill of north-west Europe. The exact stratigraphical range and distribution have yet to be established; but any record of a coarse ribbed '*Oxoplecia*' must remain suspect until the diagnostic characters are ascertained.

In his 1971 paper, Amsden made the interesting stratigraphical point that the known *Placotriplezia* in North America are confined to the Wenlock, with *Triplezia* not ranging up beyond the Llandovery. In his consideration of material from outside North America, Amsden, basing his comments on Davidson's figure (1883, pl. 8, fig. 23), observed that the single specimen of the species *T. wenlockiensis* from the Wenlock Limestone has a pseudodeltidial ridge (Amsden 1971, p. 149); but re-examination of the specimen by Bassett (1972, p. 73) showed that the pseudodeltidium is in fact flat like *Placotriplezia*, and bears no trace of any median structure. Amsden also suggested that other smooth-shelled European species such as Barrande's species *Mimulus moera* and *M. contrarius* from Bohemia could also be representatives of *Placotriplezia*. These Wenlock species have recently been re-examined by Havlíček (Havlíček and Štorch 1990, p. 58) and the flat pseudodeltidium confirmed. No smooth triplesiids have been described from the Wenlock of Gotland, but I have examined the IGT collections for triplesiids and these include a small amount of fragmentary material obtained by Dr Madis Rubel from marls of Wenlock age in south-west Estonia and which were provisionally ascribed to *Triplezia*. The sample, IKLA: 276.0-1 from the Paramaja horizon of the Jaani Stage (J1), consists of fragments of about ten valves including three well-preserved cardinalia, but no ventral valve interareas that show a complete pseudodeltidium. The three cardinalia, of which the largest is 3.1 mm wide as measured between the distal ends of the brachiophores, all possess a grooved cardinal process with a flat dorsal surface without any trace of a cardinal process hood. Thus, notwithstanding the lack of data regarding the pseudodeltidial fold, I regard these features in themselves as being sufficiently diagnostic so that, coupled with the smooth external surfaces, these Wenlock specimens from Estonia may therefore confidently be attributed to *Placotriplezia*. Thus all the European evidence presently available supports the evidence from North America that *Placotriplezia* seems to replace *Triplezia* in the Wenlock.

VARIATION IN *STREPTIS*

The development of the cardinal process type is of particular interest in the small triplesiid *Streptis*, which invariably has a monticulus on the pseudodeltidium. *Streptis* occurs most abundantly in the form of conjoined valves so that separated valves revealing the features of the interior are of relatively rare occurrence at most horizons. In the BMNH collections, amongst the large numbers of the Wenlock species *Streptis grayii* (Davidson) from Shropshire and Staffordshire, is a dorsal valve of this species in the Davidson Collection (B.8072) from Gotland in which the cardinal process possesses a hood but which is also grooved (Pl. 1, figs, 11, 14). A single dorsal valve from the Wenlock Shale at Dudley in the USNM (86311) also displays a grooved cardinal process. In his redescription of this species, Bassett (1972, p. 77) noted the grooved nature of the cardinal process and its very small hood; the latter is visible on the accompanying illustrations (pl. 17, figs 4-5), although the dorsal surface of the proximal part of the cardinal process is not visible. Transversely sectioned specimens of conjoined *S. grayii* valves (Text-fig. 1) do not, however, show the typical proximal indentation on the dorsal side as illustrated for the grooved process of *Placotriplezia praecipita* (e.g. Amsden 1971, fig. 8B), *P. waldronensis* (e.g. Amsden 1973, fig. 15F) and *Oxoplecia* sp. (Wright 1971, fig. 2e-f; and as *Ogmoplecia* in Text-fig. 2A-B herein). Instead, the dorsal side of the process is essentially flat in this region, with the groove developing later on the anterior surface as the process curves posteriorly to become directed into the ventral umbonal cavity. This was the same in all three specimens sectioned to examine the cardinal process. Thus the grooved process of *S. grayii* differs from the other grooved processes noted above. The flat proximal part is also in contrast with that of the keeled process, illustrated here for *Triplezia extans* (Text-fig. 2C-D), which



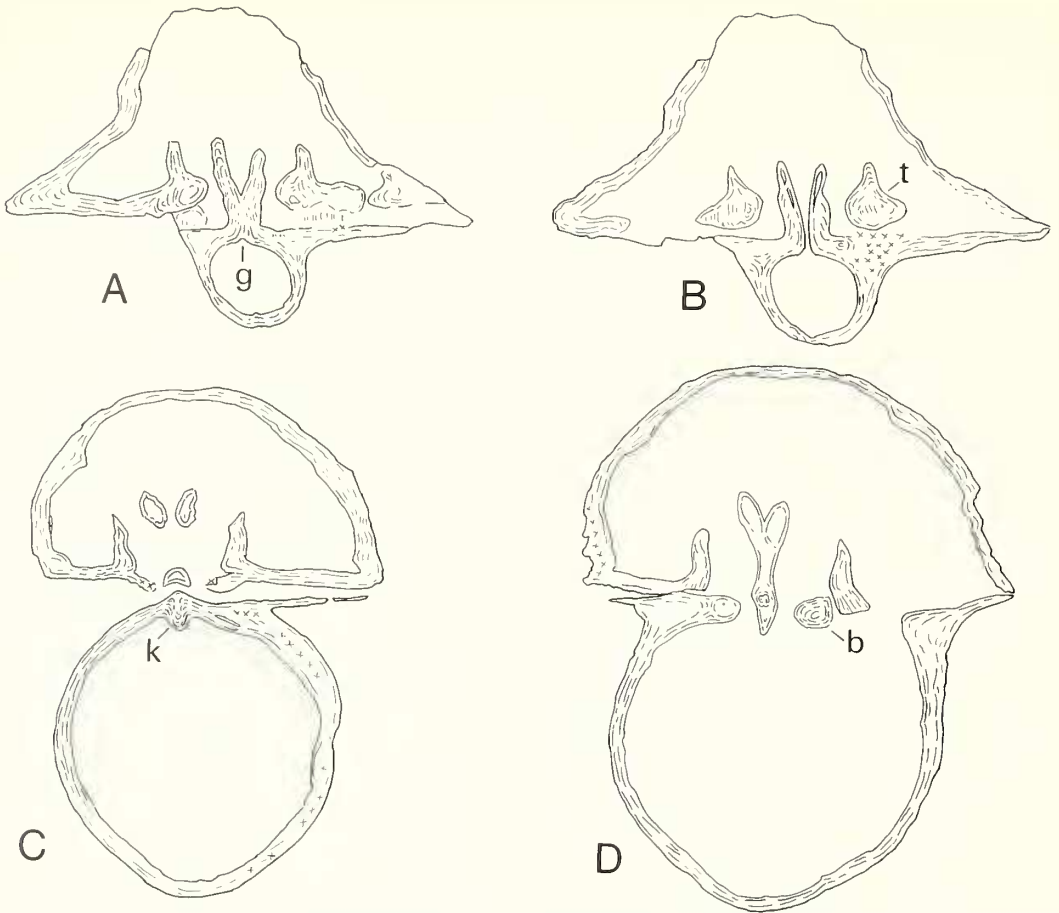
has a posterior ridge proximally that continues onto the anterior surface, with the fork only developing distally on the ventral facing surface.

But while the Wenlock *S. grayii* has a modified grooved process, a section taken of the Norwegian Early Llandovery form *S. altosinuata* Høltedahl and figured by Wright (1960, fig. 11F) shows this earlier species to be a keeled form. Similarly, the figure of Hints (1986, pl. 1, fig. 13) shows that the Late Ashgill Porkuni Stage *S. undifera* (Schmidt) from Estonia also possesses a keeled process. Since that paper was written, additional silicified material has been extracted from etchings for conodonts from Porkuni Quarry and is now in the collections of the IGT. The cardinalia of these exquisitely preserved specimens consist of very delicate, pointed, laterally directed brachiophores, well separated from a keeled cardinal process that possesses a well-developed hood. In the ventral valve, a pedicle tube with ventral margins advancing across the valve floor has been noted, such a tube having previously been recorded in *S. altosinuata* (Wright 1960) and *S. grayii* (Bassett 1972). The teeth are supported by receding dental plates, divergent to the valve floor, while the pseudodeltidium has a well-developed monticulus with an anterior invagination reflecting the presence of a curved, saddle-like plate internally.

The evidence of these forms of *Streptis* suggests either that the apparently consistent keeled process of these earlier species had evolved towards a grooved process by Wenlock times; or that the process is the more fundamental character, and that the Wenlock form developed independently from a lineage with a grooved process and converged towards the earlier *Streptis*. The latter interpretation is here regarded as demanding too much of evolutionary convergence in requiring the separate development of a species that, apart from the cardinal process, shares all its generic characters with other members of the genus. These characters are a small size, up to about 10 mm long; an ornamentation consisting of concentric lamellae that are extended into frills and crossed by radial ribs, the differing densities of which form the basis of the species; and a dorsal fold and ventral sulcus which are commonly lost in an asymmetrical twisting of the shell (hence the generic name), the end result of which is the development of a sinusoidal anterior commissure (Pl. 1, figs 5–6). The asymmetry characterizes all species, but to a varying degree. Thus although *S. altosinuata* is a species in which symmetrical forms predominate, about one in five shells in a sample of fifty-four showed some degree of asymmetry, with only one showing a sinusoidal anterior commissure (Wright 1960, p. 267). The Wenlockian *S. grayii* has an asymmetrical shell apparently invariably developed (Bassett 1972, p. 77), along with a sinusoidal anterior commissure. The St Clair Limestone Wenlock species, *S. glomerata* Ulrich and Cooper, 1936, is similarly twisted, apart from two ventral and one dorsal valves in Ulrich and Cooper's sample; Amsden (1968, p. 39) questioned the assignment of the dorsal valve to *S. glomerata*, but the specimen is probably best interpreted as a variant of that species in view of the indisputable variability of the asymmetry in other forms.

As regards intraspecific variation in *Streptis grayii*, although Bassett (1972, p. 74) recorded a pseudodeltidial fold as being present in every specimen examined, he made the point that its development was variable, between being hardly perceptible to being strong and prominent. Further, the presence of *S. grayii* of a pseudodeltidial fold in combination with a grooved cardinal process furnishes another example of the variable association of potential subfamilial characters that mitigates against any clear-cut subfamilial groupings. The distribution of these characters for some of the triplesiid taxa is illustrated in Table 1. While this covers many well-known and widespread forms, the list is far from comprehensive. In the first place many descriptions do not detail the precise form, particularly of the internal structures; and in the second, the necessary well-preserved ventral interareas and valve interiors are simply not available for description. For example, *Oxoplecia shallockiensis* (Davidson) from the early Ashgill of Girvan is a species long known, but from only a single dorsal valve exterior (Harper 1989, p. 100). Notwithstanding these gaps in the

TEXT-FIG. 1. Sequence of transverse sections to show the development of the cardinal process in a specimen of *Streptis grayii* (Davidson), taken at 0.1 mm intervals, A at 0.3 mm from the ventral umbo; ventral valve uppermost, $\times 12$. Abbreviations: b = brachiophore; cp = cardinal process; d = distal ends of cardinal process; t = tooth.



TEXT-FIG. 2. Transverse sections comparing the grooved cardinal process of *Ogmoplecia* sp. (A at 1.3 mm and B at 1.5 mm from the ventral umbo) with the keeled cardinal process of *Triplesia extans* (Emmons) (C at 1.8 mm and D at 2.25 mm from the ventral umbo). Ventral valve uppermost. All $\times 8$. Abbreviations: b = brachiophore; g = groove; k = keel; t = tooth.

information available, Table 1 does nevertheless show that the variation in these potentially supra-generic characters is such as to preclude any meaningful taxonomic grouping of the triplesiid stocks.

PSEUDODELTIDIUM AS A MEANS OF SUBDIVISION

From the earlier discussion it is clear that while the characteristic of the presence or absence of a pseudodeltidial fold may be of systematic value at generic level, its use by Amsden (1968) to subdivide the family into two subfamilies is unacceptable, as the structure is too variable to allow any such clear-cut division. Additional examples are to be found in *Amphiplecia* and *Grammoplecia* (both Wright and Jaanusson 1993). Both show variation in the degree of development of the monticulus, which in the former is absent to weak and in the latter commonly developed posteriorly but fading with growth: this may be associated with the change in attitude of the interarea. The feature of a keeled or grooved cardinal process, while again quite distinct and useful as a valid generic character in some stocks, also shows itself to be of variable form in others; the basically keeled processes of *Oxoplecia multicostellata* Cooper and *Cliftonia tubulistriata* (Savage) fall into

TABLE 1. Distribution of potential supra-generic characters in some triplesiid taxa.

Taxon and age	Monticulus	Pedicle tube	Cardinal process	Hood
<i>Triplesia</i> spp. (M. Ordovician–Llandovery)	Present	Absent, passage	Keeled	Present
<i>Placotriplesia</i> spp. (Wenlock)	Absent	Absent	Grooved	Absent
<i>Streptis undifera</i> (Ashgill) and <i>S. altosinuata</i> (Llandovery)	Present	Short	Keeled	Present
<i>S. grayii</i> (Wenlock)	Present, but variably developed	Short	Grooved	Present
<i>Ogmoplectia</i> spp. (Ashgill)	Absent, but may develop in some shells	Absent, passage	Grooved	Absent
<i>Cliftonia tubulistriata</i> (Ashgill)	Present, may be lost anteriorly	Present	Keeled variably	Absent
<i>Oxoplectia multicostellata</i> (Caradoc)	Present, but lost anteriorly	Passage	Keeled variably	Absent
<i>Bicuspina</i> spp. (Llandeilo–Caradoc)	Present	Present, long	Keeled low	Present
<i>Plectotreta lindstroemi</i> (Wenlock–Ludlow)	Passage	Present	Grooved	Present

this latter category. Likewise, while the associations of these features, keeled process with pseudodeltidial fold and grooved process with smooth pseudodeltidium, are typical, other combinations do occur. Thus neither a single nor a set of characters has been found that can be used to produce a useful subdivision of the family into subfamilies. Not only is there variation in these particular characters, but a high degree of fluidity is present in various aspects of shell morphology among the genera, e.g. asymmetry in *Streptis*; radial ornament in *Onychotreta*. Indeed a commonly plastic shell form seems to be a hallmark of the family; and it is worth a reminder that while the secondary shell substance is apparently always lamellar and predominantly impunctate, the occasional stock does possess well developed pseudopuncta (Wright 1970).

ORNAMENT AS A MEANS OF SUBDIVISION

Two main points were made by Havlíček (*in* Havlíček and Štorch 1990, p. 56) in his discussion of the Triplesiacea. First, regarding the taxonomic value of the pseudodeltidial fold, his quite independent view concurs with my own expressed above, i.e. that the structure is of value for the generic separation of *Placotriplesia* but is 'of little use when classifying triplesiids into higher systematic units' (Havlíček and Štorch 1990, p. 57). This last remark is based on the loss of fold occurring 'at least in three terminal links' of lineages. He further noted that the loss of the fold may be assumed to be a general trend in the evolution of upper Wenlock members of the suborder. *Streptis*, and also *Plectotreta*, would appear to be stocks that did not succumb to this trend; while *Ogmoplectia* showed the loss of the monticulus very much earlier.

Secondly, Havlíček (*in* Havlíček and Štorch 1990) made the radical proposal that the superfamily Triplesiacea may be subdivided into three families based on the shape of the shell and the ornamentation. The proposed families are the Triplesiidae s.s., containing the genera with smooth shells; the Oxoplectiidae, containing the costate, costellate or imbricate genera; and the Onychotretidae, to contain those of claw-like outline with an extremely elongate ventral beak, i.e. the unusual and very variable *Onychotreta*. This proposal needs some consideration for, as

indicated previously, the features around the ventral umbo and the dorsal cardinalia are the characters normally regarded as being of taxonomic significance at family level, with a role at higher levels for shell punctuation and fabric. Ornamentation and variation in shape and other details are traditionally viewed then as having lower taxonomic significance. With regard to ornamentation, for example, that of *Eichwaldia* and *Dictyonella* could hardly be more dissimilar, with the fine concentric growth lines of the former contrasting with the 'very peculiar' net-like ornament of the latter (discussed in Wright 1981); but the two are so alike in all other respects that it is inconceivable that they should be placed in separate families or even subfamilies.

However, while accepting that the traditional view is not immutable, a problem with the new proposal is the inherent variation within the Triplesiacea that upsets the neat pigeon-holing of the two main smooth/ornamented groups. The following examples illustrate the point.

1. Williams's (1974) genus *Caeroplecia* is a costate form, distinguished from *Oxoplecia* by having a concentric ornament of rounded fila instead of lamellose growth lines, and also by its delayed rib development. Apart from the type species, Williams (1974, p. 123) included *Oxoplecia mutabilis* Williams, 1955, the original description of which emphasized the late development of the ribs. Williams pointed out that 'immature specimens (less than 14 mm wide) bear only marginal costae and much of the surface is without radial ornamentation' (Whittington and Williams 1955, p. 412). Here then are forms, along with, for example, several of the *Oxoplecia* species illustrated by Cooper (1956), in which either smooth forms develop ribs with age or else a ribbed form has undergone a neotenus suppression of the ribbing. Either way it casts doubt on the prudence of separating the rough from the smooth!

2. While *Onychoplecia* is defined by Cooper (1956, p. 529) as having a surface marked by concentric growth lines only, the earliest species, from the Llanvirn Table Head Group of Newfoundland, does show fine radial ribs in what Cooper described as exfoliated specimens (Cooper 1956, p. 532), although these are present on the *holotype* which is described as a perfect specimen, and the undulations visible on the lateral commissure (Cooper 1956, pl. 100, fig. 4) further suggest that this is a genuine feature of the external surface. Another sample, from the Hirnantian of northern England and which is identified as *Onychoplecia* sp. nov. by Temple (1968, p. 33), includes some specimens which develop marginal ribs. Temple considered these to be variant individuals of the essentially smooth-shelled species. Thus *Onychoplecia* could also be viewed as straddling two of the proposed families.

3. The genus *Grammoplecia*, described from the Ashgill Boda Limestone of central Sweden but including a number of other forms of upper Ordovician age (Wright and Jaanusson 1993), differs generically from *Triplesia* only in its capillate ornament, with the external form of the two type species having a particularly strong resemblance to each other. The fine ornament would however exclude the new genus from Havlíček's (Havlíček and Štorch 1990) smooth shelled Triplesiidae, a separation which would appear as anomalous as placing the well-known smooth Silurian pentameride *Stricklandia lens* in a separate family from the ribbed *Costricklandia lirata*.

4. Three other forms of the diverse triplesiid assemblage in the Ashgill Boda Limestone that were not known to Havlíček when he proposed his subdivision further demonstrate the impracticability of separating the smooth genera from those with variously developed concentric and radial ornamentations. *Amphiplecia* Wright and Jaanusson, 1993, is, like *Caeroplecia*, a ribbed form in which the ribs do not develop until after a smooth phase which encompasses the first 4–5 mm of growth, again producing a potential problem when classifying young shells in the proposed new families. A further problem is highlighted by a single adult specimen, which has been located in the RMS collections, from Kallholn Quarry, Sweden and which is identical with *Amphiplecia* (complete with the strikingly distinct shape where one-half of the shell is twisted with respect to the other along the mid-line of the shell) except that it is essentially devoid of radial ornament (Wright and Jaanusson 1993, fig. 4P–Q, T). This smooth individual is treated as being simply an aberrant member

of the *Amphiplecia* population, yet it would need to be placed in a separate family from its fellows according to the proposed new familial classification. A third problematic form in this assemblage is one which is smooth for the first 10 mm of growth, anterior to which ribs develop on the fold and in the sulcus, typically with 4 or 5 on the fold and one less in the sulcus, but which may be completely absent laterally (Pl. 1, figs 10, 12, 15). This form, which has a smooth pseudodeltidium lacking a monticulus, is known so far from only a dozen specimens of very variable preservation with information on the interiors lacking. Accordingly, although its distinct assemblage of characters indicate a new genus, it is at present considered best left under open nomenclature. But as regards Havlíček's familial classification, this is another form the placement of which would be uncertain.

5. A further example which presents a case similar to the smooth *Amphiplecia* specimen is an apparently smooth shell described by Poulsen (1943, p. 22) as *Streptis laevis*, a species distinguished from others of the genus primarily by the absence of radial ornamentation.

6. The extreme variation in *Onychotreta* includes the species *O. plicata* Ulrich and Cooper for which Amsden erected the subgenus *Lissotreta*. These shells are characterized (Amsden 1968, p. 37) by 'an exterior which is, excluding the pedicle valve sulcus and brachial valve fold, nearly smooth'. While this is here interpreted as one morphological expression of a highly plastic stock, a pigeon hole classificatory key based on ornament would technically place the form with the grouping containing the other smooth triplesiids, the surface of which is only modified by fold and sulcus. The proposed classification of Havlíček avoids this particular problem by giving *Onychotreta* a family of its own based in this case on its peculiar outline. *Onychotreta* is only known to occur in beds of Wenlock age, in Arkansas (Ulrich and Cooper, 1936), Oklahoma (Amsden 1968) and Bohemia (Havlíček and Štorch 1990). Re-examination of the single dorsal valve ascribed to this genus from the Ashgill of Ireland by Mitchell (1977, p. 66) shows that it is not an *Onychotreta* as it does not have the triplesiid cardinalia, although externally it does show similarities to the triplesiids now placed in *Amphiplecia*.

In summary, the known anomalies suggest that a separate family based on a smooth shell surface is far from satisfactory and would overlap with the family based on ornamented stocks, while the aberrant *Onychotreta*, stratigraphically appearing only in the final flourish of the superfamily, does not, in my opinion, merit separate familial status on present evidence. Likewise, the subdivision of the family based on the presence or absence of a monticulus cannot be sustained; in this connection it is of interest to note that the development of this structure has not been regarded as a suprageneric character in either the Stropheodontidae (Williams 1953) or the Derbyiaceae (Cooper and Grant 1974). Accordingly, the view is taken here that the constituent genera are best assigned to the single undivided family Triplesiidae.

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